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Joseph P. Dietrich [a], Deborah A. Boylen [a], Donald E. Thompson [b], Erik J. Loboschefsky [b], Claudia F. Bravo [b e], Dina K. Spangenberg [c], Gina M. Ylitalo [c], Tracy K. Collier [c], Derek S. Fryer [d], Mary R. Arkoosh [a] & Frank J. Loge [b]

[a] National Oceanic and Atmospheric Administration-Fisheries, Northwest Fisheries Science Center, Newport Research Station, 2032 Southeast OSU Drive, Newport, Oregon, 97365, USA

[b] Department of Civil and Environmental Engineering, University of California Davis, 1 Shields Avenue, Davis, California, 95616, USA

[c] National Oceanic and Atmospheric Administration-Fisheries, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington, 98112, USA

[d] U.S. Army Corps of Engineers, Walla Walla District, 201 North 3rd Avenue, Walla Walla, Washington, 99362, USA

[e] Retired

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ARTICLE

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Joseph P. Dietrich* and Deborah A. Boylen
National Oceanic and Atmospheric Administration–Fisheries, Northwest Fisheries Science Center, Newport Research Station, 2032 Southeast OSU Drive, Newport, Oregon 97365, USA

Donald E. Thompson, Erik J. Loboschefsky, and Claudia F. Bravo[1]
Department of Civil and Environmental Engineering, University of California Davis, 1 Shields Avenue, Davis, California 95616, USA

Dina K. Spangenberg, Gina M. Ylitalo, and Tracy K. Collier
National Oceanic and Atmospheric Administration–Fisheries, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Derek S. Fryer
U.S. Army Corps of Engineers, Walla Walla District, 201 North 3rd Avenue, Walla Walla, Washington 99362, USA

Mary R. Arkoosh
National Oceanic and Atmospheric Administration–Fisheries, Northwest Fisheries Science Center, Newport Research Station, 2032 Southeast OSU Drive, Newport, Oregon 97365, USA

Frank J. Loge
Department of Civil and Environmental Engineering, University of California Davis, 1 Shields Avenue, Davis, California 95616, USA

Abstract

Various methods have been developed to mitigate the adverse effects of the Federal Columbia River Power System on juvenile Pacific salmon out-migrating through the Columbia River basin. In this study, we found that hatchery-reared spring Chinook salmon *Oncorhynchus tshawytscha* in the river are in varying degrees of health, which may affect delayed mortality and the assessment of the effectiveness of management actions to recover listed stocks (e.g., barging fish downstream versus leaving fish in the river). A laboratory disease challenge with *Listonella anguillarum* was completed on fish from Rapid River Hatchery and Dworshak National Fish Hatchery (NFH) with different out-migration histories: (1) transported by barge, (2) removed from the river before barging, or (3) left to travel in-river. Barged fish from Rapid River Hatchery experienced less mortality than fish from Dworshak NFH. No statistical differences were found between the hatcheries with fish that had in-river out-migration histories. We suggest that the stressors and low survival associated with out-migration through the hydropower system eliminated any differences

*Corresponding author: joseph.dietrich@noaa.gov
[1]Retired.
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that could have been present. However, 18–25% of the fish that were barged or collected before barging died in the laboratory before the disease challenge, compared with less than 2% of those that traveled in-river. Owing to disproportionate prechallenge mortality, the disease-challenged populations may have been biased; thus, they were also considered together with the prechallenge mortalities. The synthesis of prechallenge and disease-challenged mortalities and health characteristics evaluated during out-migration indicated that the benefit of barging was not consistent between the hatcheries. This finding agrees with adult survival and delayed mortality estimates for the individual hatcheries determined from adult returns. The results suggest that the health status of fish and their history before entering the hydropower system (hatchery of origin and out-migration path) are critical variables affecting the conclusions drawn from studies that evaluate mitigation strategies.

The Columbia River basin in the Pacific Northwest of the United States provides critical habitat for threatened and endangered Chinook salmon *Oncorhynchus tshawytscha*. Thirteen stocks, or evolutionarily significant units, from this region are threatened or endangered, including the Snake River spring Chinook salmon (Waples 1991; NRC 1996). Factors contributing to the decline of Pacific salmon populations include habitat degradation, overharvest, hydropower operation, and hatchery production (NRC 1996). Although the Federal Columbia River Power System (hydropower system) is instrumental in providing power, irrigation water, flood protection, navigation, and recreation, the system has substantially affected salmon migration. Some of the Columbia River basin's threatened or endangered stocks must migrate past as many as eight dams. Aside from restricting access to adult reproductive habitat, the hydropower system contributes to losses of juvenile stocks during river out-migration (Raymond 1988). In the absence of the hydropower system, mortality of out-migrant salmon in the river and estuary may occur owing to predation, injury, and disease. The hydropower system may further exacerbate these causes of mortality, as well as impose additional sources of direct and delayed mortality. Direct mortality is defined herein as death that takes place during the life stage when the stressor was imposed. Delayed mortality is defined herein as death that occurs at a life stage after that when the stressor was imposed.

A number of actions have been taken to mitigate direct and delayed mortality in out-migrant salmon, including construction of juvenile fish passageways that bypass Columbia and Snake river dams, transportation (barging) of juvenile fish through the dams, predator control, flow augmentation, and reservoir drawdown (Muir et al. 2001; Ruckelshaus et al. 2002). However, the specific effects of these actions on population numbers are currently not well quantified. In addition, these actions may induce levels of stress that exacerbate delayed health effects associated with predator avoidance, disease susceptibility, growth, and delayed mortality. For example, barging juvenile salmon is believed to induce stress associated with handling and crowding, and the juvenile fish passageways have caused mechanical injuries such as bruising and descaling, and exposure to supersaturated gasses (NRC 1996; Budy et al. 2002). Evidence of delayed mortality has been associated with salmon populations that have been barged as well as fish that use increasing numbers of fish passageways around dams (Sandford and Smith 2002; DeHart et al. 2009).

Tagged hatchery-reared salmon in the hydropower system provide a basis for assessing the magnitude of direct and delayed mortality. The direct mortality of tagged fish between the Lower Granite Dam tailrace to the Bonneville Dam tailrace can be calculated based on detections at individual dams. The direct in-river mortality rate estimated for hatchery-raised spring Chinook salmon is 50–60% (Williams et al. 2001; Berggren et al. 2006), whereas the assumed direct mortality of barged juvenile salmon is less than 2% (Budy et al. 2002; Berggren et al. 2003).

An estimate of the magnitude of delayed mortality is less straightforward owing to multiple factors that contribute to juvenile mortality below Bonneville Dam and the absence of large-scale tag detections until salmon return as adults 2–4 years later. When adults return to the hydropower system, smolt-to-adult return (SAR) rates (i.e., the ratio of the number of adults returning to a location to the number of smolts leaving that location) can be calculated for specific out-migration histories. Smolt-to-adult returns and the survival of juvenile Chinook salmon through the hydropower system are then used to estimate the differential delayed mortality (D) of one migratory group relative to another, that is,

$$D = \frac{\mathrm{SAR(BRG)}}{V_{\mathrm{brg}}} \Big/ \frac{\mathrm{SAR(IR)}}{V_{\mathrm{ir}}}, \tag{1}$$

where V_{ir} is the survival rate of in-river out-migrants to Bonneville Dam and V_{brg} is the survival rate of transported juveniles. The presence of V_{brg} and V_{ir} are intended to normalize the SAR rate of transported (SAR[BRG]) and in-river (SAR[IR]) out-migrants for direct mortality in the hydropower system. Hence, a value of 1.0 for D implies that there is no difference in post-hydropower system mortality in either group. Annual V_{ir} values have been roughly 0.5 in hatchery fish originating from the Snake River basin based on multiple mark–recapture survival estimates, and V_{brg} has ranged from 0.88 to 0.98, but survival for all transported fish once on the barge is assumed to be 0.98 as per Berggren et al. (2003) (DeHart et al. 2009). The annual values of D for tagged spring Chinook salmon originating

from Dworshak National Fish Hatchery (NFH) and Rapid River Hatchery are consistently less than a value of 1 (Berggren et al. 2006), implying that delayed mortality is greater for transported fish. Hence, *D* values suggest that barging operations represent a significant stressor to salmon that results in greater delayed mortality than in salmon with in-river out-migration histories (Bouwes et al. 1999).

Arkoosh et al. (2006) conducted a study during the 2002 out-migration year to examine the health of Rapid River Hatchery Snake River spring Chinook salmon as affected by bypass history and barging. The health of out-migrants was assessed in terms of the difference in the incidence of mortality among fish, categorically grouped into no-bypass, bypass, and transportation out-migration histories, in response to challenge with the pathogenic marine bacterium *Listonella anguillarum*, the causative agent of vibriosis, during seawater holding. They found that the cumulative mortality associated with barged fish was significantly less than in-river fish with zero, single, or multiple bypass out-migration histories. Within the disease challenge study design, disease susceptibility was viewed as a measure of physiological health and the potential for delayed mortality among fish with different out-migration histories. During out-migration, an increase in disease susceptibility could result in adverse population effects owing to increased disease-induced mortality, increased predation mortality, and reduced reproductive potential (Sindermann 1990; Congleton et al. 2000; Schreck et al. 2006). Overall, the Arkoosh et al. (2006) study indicates that in-river out-migrants (traveling through one or more bypass structures) are more susceptible to infectious disease than are juveniles transported through the hydropower network, and hence, more prone to delayed mortality. Although this study was completed in a single out-migration year with a single source of juvenile salmon, Arkoosh et al. (2006) suggests that barging out-migrants mitigates the effect of the hydropower system on delayed mortality, and more generally, improves the overall health status of fish entering the estuary.

In the present study, we compared the disease susceptibility of Snake River spring Chinook salmon originating from Rapid River Hatchery and Dworshak NFH that had experienced barged and in-river out-migration histories. In addition, we collected and analyzed a suite of characteristics of out-migrants from the two hatcheries to further characterize the health status of the out-migrating fish. Consequently, the results from this study provide insights into the effect of fish origin and early out-migration, as well as out-migration history on health, delayed mortality, and possibly adult returns.

METHODS

Study Area

The study area encompassed the spring Chinook salmon migration routes from Dworshak NFH and Rapid River Hatchery, both located in Idaho (Figure 1). From Rapid River Hatchery, located on the Salmon River at river kilometer (rkm) 149.7, the

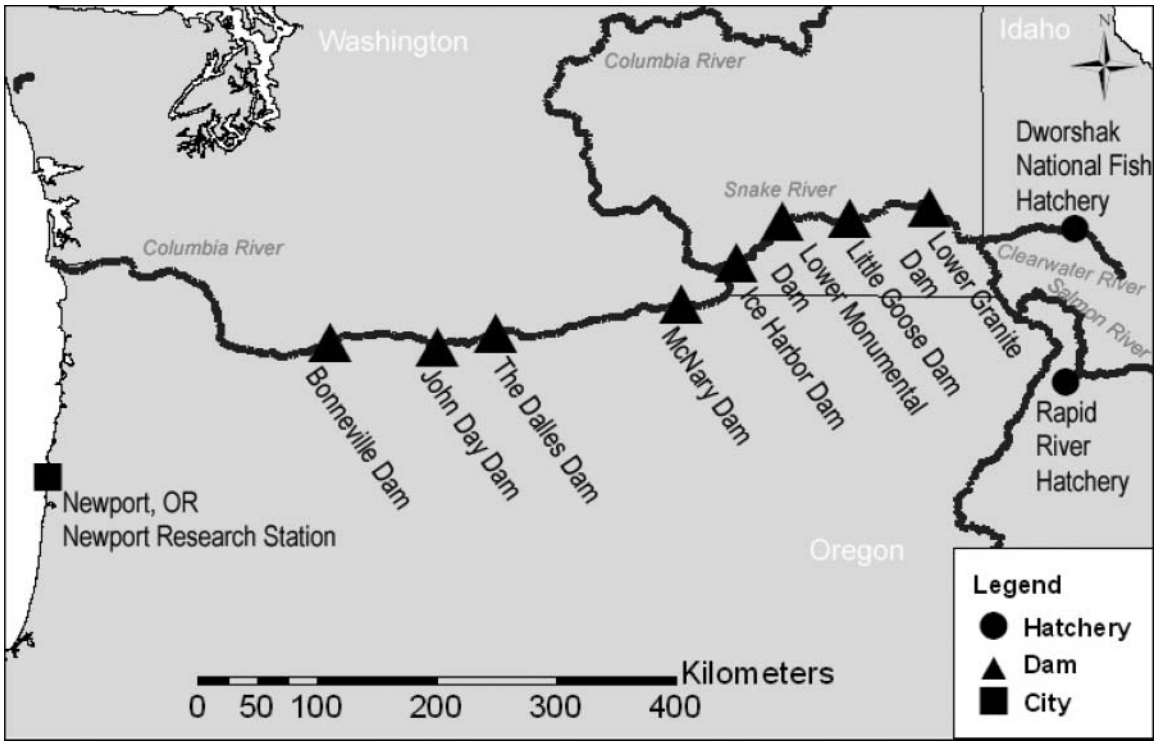

FIGURE 1. Migration corridor for Chinook salmon in the Snake and Columbia rivers from Dworshak National Fish Hatchery and Rapid River Hatchery to the Pacific Ocean.

migration route is approximately 975.5 km to the Pacific Ocean. At Rapid River Hatchery juveniles began their migration from the rearing pond at will (i.e., volitional release) on March 17, 2006. From Dworshak NFH, located on the Clearwater River at rkm 66.0, the migration route is approximately 812.9 km to the Pacific Ocean. In 2006, personnel at Dworshak NFH released fish from rearing raceways on March 27 and 29.

Out-migrants from both hatcheries encountered eight hydroelectric projects (Figure 1): four on the lower Snake River, including Lower Granite (Snake River kilometer [SRkm] 173.0), Little Goose (SRkm 113.2), Lower Monumental (SRkm 67.0), and Ice Harbor (SRkm 15.6); and four on the Columbia River, including McNary (Columbia River kilometer [CRkm] 470.0), John Day (CRkm 247.1), the Dalles (CRkm 308.3), and Bonneville (CRkm 235.2).

Fish Collection and Care

Collection of out-migrants in the hydropower system.—Approximately 126,000 juvenile spring Chinook salmon from Dworshak NFH ($n = 63{,}871$) and Rapid River Hatchery ($n = 62{,}243$) were tagged with passive integrated transponder (PIT) tags before their 2006 hatchery release. Tagging efforts were performed by BioMARK (Boise, Idaho) for this study or as part of the Fish Passage Center's Comparative Survival Study. Chinook salmon that were PIT-tagged were separated from the population passing through the Lower Granite Dam and Bonneville Dam Second Powerhouse Bypass Systems with a PIT tag separation-by-code (SbyC) system located at each dam. These fish were diverted into temporary holding pens where they were scanned for the presence of PIT tags, and nonstudy fish were removed and released. Each experimental fish was anesthetized with a nonlethal dose (25–50 mg/L) of tricaine methanesulfonate (MS-222; Sigma-Aldrich) and length and weight were recorded and condition factors were calculated (Nash et al. 2006). The fish were held for a minimum recovery period of 18 h in tanks supplied with flow-through river water at a density less than 20 g/L before being transported from Lower Granite Dam either by barge to Bonneville Dam or truck to the Newport Research Station (NRS; Newport, Oregon). Fish were held, on average, for a period of 1 to 2 d before transport. Fish were trucked to NRS in a 1,900-L stainless steel tank containing conditioned recirculated water. Water quality characteristics in the transport tank were periodically monitored during transit and never exceeded levels recommended by Wedemeyer (1996): temperature, $<12.5^{\circ}$C; dissolved oxygen, >6 mg/L; pH, 6–9; carbon dioxide, <5–10 mg/L; un-ionized ammonia, <0.02 mg/L; nitrate, <1.0 mg/L; and nitrite, <0.1 mg/L. Water temperature was controlled through the periodic addition of ice. The fish density in the transport tank never exceeded 10 g/L.

Experimental cohorts.—Chinook salmon out-migrants collected from the river system were grouped into three experimental cohorts (Lower Granite, in-river, and barged) based on their out-migration history. Efforts were made to collect fish for all cohorts over the entirety of the out-migration season. The "Lower Granite" cohort contained fish collected at Lower Granite Dam. Fish within this cohort experienced one juvenile passageway at Lower Granite Dam as well as an out-migration distance of 117.5 or 280.1 rkm from Dworshak NFH or Rapid River Hatchery, respectively. The "in-river" cohort contained fish collected at Bonneville Dam. Fish within this cohort experienced one to seven juvenile passageways, zero to seven spillway or turbines, as well as an out-migration distance of 577.9 or 740.5 rkms from Dworshak NFH or Rapid River Hatchery, respectively. Finally, the "barged" cohort contained fish that were collected at Lower Granite Dam juvenile passageway, placed in approximately 810-L net-pens suspended in barge holds, and transported by barge to Bonneville Dam. The fish densities in the net-pens ranged from 7.6 to 8.6 g/L. Fish within this cohort experienced 460.4 rkms of transport in a barge hull shared with other out-migrating, run-at-large populations (e.g., wild and hatchery steelhead *O. mykiss* [anadromous rainbow trout] and Chinook salmon) loaded at Lower Granite, Little Goose, and Lower Monumental dams at densities less than 60 g/L. Transit from Lower Granite to Bonneville Dam generally took from 36 to 44 h. Barged and in-river cohorts experienced identical travel times from Bonneville Dam to NRS in the truck transportation tank (ca. 4.5 h), whereas the travel time for the Lower Granite cohort by truck to NRS was nearly three times longer (ca. 13 h).

Collection of hatchery reference fish.—Yearling hatchery spring Chinook salmon (approximately 1,100 "reference" fish) were obtained from Leaburg Hatchery (Leaburg, Oregon) to serve as a biological reference throughout the disease challenge experiments to assess reproducibility between experiments. The fish were transported to NRS in a 1,900-L stainless steel tank containing conditioned recirculated water. All water quality characteristics were within acceptable limits during transport (per Wedemeyer 1996), and the fish arrived at NRS within 3.5 h of loading.

Fish care at NRS.—Before the disease challenge, fish were fed a diet of semimoist food pellets (Bio-Oregon; Warrenton, Oregon) three times per day to satiation. Water quality characteristics were monitored in individual tanks on a daily basis and modifications were made to individual tank operation as necessary. Ectoparasite outbreaks occurred in tanks containing Lower Granite and barged fish within the first 2 weeks of arrival at the NRS, which necessitated treatment. For consistency, all fish in each of the cohorts (Lower Granite, barged, and in-river) were treated for ectoparasites with 0.025% formalin (250 μL formalin/mL of water) for 1 h under static conditions with supplemental aeration, repeated over three consecutive days (Noga 1996). Saltwater introduction was also included in the treatment regimen and began at the time of formalin treatment. Transition from freshwater to saltwater occurred by gradually increasing the salinity in individual tanks over a weeklong period until 34% absolute salt concentration was achieved. Owing to differences in fish out-migration timing and transport timing, the onset of treatment for each fish ranged from 2 to 22 d, 4 to 18 d, and 2 to 12 d since collection for the Lower Granite, barged, and

in-river cohorts, respectively. Throughout this treatment process, any fish with observable fungal-like growth were culled from the population on a daily basis. The outbreak of mortalities during holding ceased once the formalin treatment and saltwater transition was completed.

Lethal Concentration Challenge

A 9-d lethal concentration (LC) challenge was performed as per Arkoosh et al. (2005) with Chinook salmon exposed to seven increasing concentrations of *Listonella anguillarum* in trypticase soy broth (TSB) with 1.5% NaCl (4×10^2 to 4×10^7 colony-forming units [CFU]/mL) to identify the pathogen concentration at which 50% of the reference fish experienced mortality (LC50). This LC50 value was to be used in the subsequent disease challenge. The LC challenge tanks contained approximately 70 fish each, composed of 10 reference fish and 20 fish from each of the experimental cohorts (barged, Lower Granite, and in-river). Fish from the experimental cohorts were included in the LC challenge to mimic the conditions of the subsequent challenge, as well as to determine whether the selected LC50 value would be appropriate. Each tank of fish experienced a 1-h bath exposure to *L. anguillarum* in 41.6 L of seawater (i.e., approximate densities of 50 g fish/L). After exposure, the fish were transferred to 427-L tanks supplied with 7 L/min of seawater for a 9-d observational period. Three replicate tanks were used for each pathogen concentration, except at the highest concentration, which had two replicate tanks. In addition, two, replicate, pathogen-free control tanks were exposed to sterile TSB. Mortalities were collected twice daily. For each dead fish, PIT tag identifications were gathered using a Destron-Fearing portable transceiver (model FS2001F-ISO). Before the start of the LC challenge, the fish had been held in the laboratory for periods of 29, 29–51, 23–47, or 26–34 d for reference, Lower Granite, barged, and in-river cohorts, respectively.

Disease Challenge

A disease challenge experiment was conducted as per Arkoosh et al. (2005). Specific details unique to this study are provided below. During the disease challenge, 21 replicate tanks of 67 fish each were exposed to *L. anguillarum* at the LC50 concentration of 8.0×10^4 CFU/mL, as determined in the LC challenge, and five replicate tanks were used as pathogen-free controls exposed to sterile TSB. Each tank was composed of 20 fish from each of the experimental cohorts (barged, Lower Granite, and in-river) and seven reference fish. Otherwise, the same experimental procedures were used in the disease challenge as in LC challenge. The start of the disease challenge occurred roughly 6 weeks after the last fish received formalin treatment, with fish held in the laboratory for periods of 58, 58–80, 54–76, or 55–63 d for reference, Lower Granite, barged, and in-river cohorts, respectively.

Survival curves for each of the Lower Granite, barged, and in-river cohorts were generated by means of the Kaplan–Meier method for fish in the controls and exposed to *L. anguillarum* during the disease challenge as well as before any challenge. Survival curves were generated across all replicate tanks for fish originating from Dworshak NFH or Rapid River Hatchery within a given experimental cohort to evaluate the potential effect of out-migration history on disease susceptibility. Significant differences between survival curves were assessed by means of the Mantel method for the log-rank chi-square test with the null hypothesis of a common survival curve. Systat12 software (Systat Software, Inc.; Chicago, Illinois) was used to generate all survival curves and perform log-rank chi-square tests with the significance level α set at 0.05 in all comparisons. During the challenges, the incidence of mortality in control groups of all cohorts was less than 5% over the course of the 14-d observational period. Furthermore, the mortalities in the control tanks were not subtracted from the mortalities in the treatment tanks before statistical analyses or during the graphical and tabular presentation of the results.

Prevalence of Natural Infectious Diseases in Out-migrants

Spring Chinook salmon released in 2006 from Dworshak NFH and Rapid River Hatchery were tested for infectious diseases during rearing. At Rapid River Hatchery, fish were tested six times in samples sizes of 8–20 fish at the Eagle Fish Health Laboratory of the Idaho Department of Fish and Game (IDFG; Eagle, Idaho). At Dworshak NFH, fish were tested once before release with a sample size of 60 fish at the Idaho Fish Health Center (Ahsahka, Idaho). Fish health inspection and diagnostic sampling of fish from both hatcheries for bacterial, viral, and protozoan pathogens followed American Fisheries Society Fish Health Section Blue Book protocols (USFWS and AFS–FHS 2005).

At three intervals during laboratory holding before the LC challenge, subsets of mortalities from the barged (61 fish) and Lower Granite (36 fish) cohorts held at NRS were sent to the Oregon Department of Fish and Wildlife (ODFW) for pathology analyses. In addition, 52 Dworshak NFH and 60 Rapid River Hatchery fish within the in-river cohort were collected and sacrificed at Bonneville Dam on May 17, 2006, and submitted for viral analysis (i.e., viral hemorrhagic septicemia virus [VHSV] and infectious hematopoietic necrosis virus [IHNV]). Fish health inspection and diagnostic sampling for bacterial, viral, and protozoan pathogens at the ODFW Fish Health Services also followed Blue Book protocols (USFWS and AFS–FHS 2005). Exams included identifying visual signs of pathology, such as body and fin damage, swollen abdomens, internal organ appearance, and overt external bacterial or fungal growth. Viral assays were also completed on pooled (1–4 fish per pool) sample tissue (kidney and spleen were always used, pyloric caeca was used in 18.5% [29 of 156] of the pools) suspensions.

Chemical Analyses of Lipids

Composite samples of five whole bodies were used to determine the total amount of extractable lipid (whole-body lipid fraction) and lipid classes (e.g., triglycerides) by thin-layer

chromatography with flame ionization detection as described in Ylitalo et al. (2005) as indicators of fish health and energy reserves during out-migration. Three composites of five fish per hatchery were collected at separate times during the out-migration period from each of the cohorts: Lower Granite (April 17 and 29 and May 9); barged (April 24 and 25 and May 3); and in-river (May 9, 20, and 23). Samples were placed on ice and transported immediately to the NRS where they were frozen and stored at −80°C until analyzed.

A one-way analysis of variance (ANOVA) that used the Tukey–Kramer honestly significant difference (HSD) multiple comparison test (Zar 1999) on arcsine transformed data was performed to determine significant differences in the measured lipid concentrations between the Lower Granite, barged, and in-river cohorts. The significance level α was set at 0.05 in all comparisons of mean concentrations. The computer program JMP (SAS Institute, Inc., Cary, North Carolina) was used to perform these analyses.

RESULTS

Disease Challenges

Incidence of mortality and pathology investigations before disease challenge.—Chinook salmon from the Lower Granite, barged, and in-river cohorts arrived at the NRS over a 30-d period owing to differences in out-migration timing through the Snake and Columbia rivers. Within the first 2 weeks of holding, external signs of fungal-like infection occurred, concurrent with an increase in mortalities (Figure 2). Subsets of the mortalities from the barged and Lower Granite cohorts submitted for pathological examination indicated numerous fungal hyphae and IHNV infections. *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD), was not detected in any of the fish submitted for analysis. In response to the fungal infection, all cohorts were treated with formalin and transitioned to saltwater, as previously described. The mortalities ceased before the start of the LC and disease challenges.

The incidence of mortality was significantly greater for fish in the Lower Granite and barged cohorts (i.e., 18.0% and 25.0%, respectively) before the LC challenge than for in-river fish (i.e., 1.7%; Table 1). Kaplan–Meier survival analysis also indicated significant differences in survival based on the date of barge or truck transport with the barged and Lower Granite cohorts, but not in-river cohorts. Survival was lowest when fish were transported in the middle of their out-migration (data not shown). Although there was minimal difference in the incidence of mortality between in-river fish originating from either Dworshak NFH and Rapid River Hatchery (2.0% and 1.3%, respectively), we did observe significant differences in mortality within barged and Lower Granite fish originating from different hatcheries ($P < 0.05$; Table 2). Before the LC challenge, fish from Dworshak NFH in the barged (31.2%) and Lower Granite cohorts (29.2%) had greater mortality than did fish from Rapid River Hatchery in their respective cohorts (21.3% and 10.0%, respectively). The significantly greater mortality observed among Dworshak NFH fish than among Rapid River Hatchery fish is contrary to pathology investigations at the time of release. No bacterial or viral pathogens were found among Dworshak NFH fish, while the causative agents of motile *Aeromonas* septicemia (*Aeromonas hydrophila*; 58.3%) and cold water disease (*Flavobacterium psychrophilum*; 41.6%) were found among Rapid River Hatchery fish. Neither of the hatcheries reported detecting BKD in any of the fish screened before release. However, an impromptu viral survey of Dworshak NFH and Rapid River Hatchery fish collected from the Bonneville Dam bypass late in their migration (May 15 and 16) indicated Rapid River Hatchery fish had an estimated IHNV prevalence of 1.6% and the Dworshak NFH fish had an estimated IHNV prevalence of 5.7%.

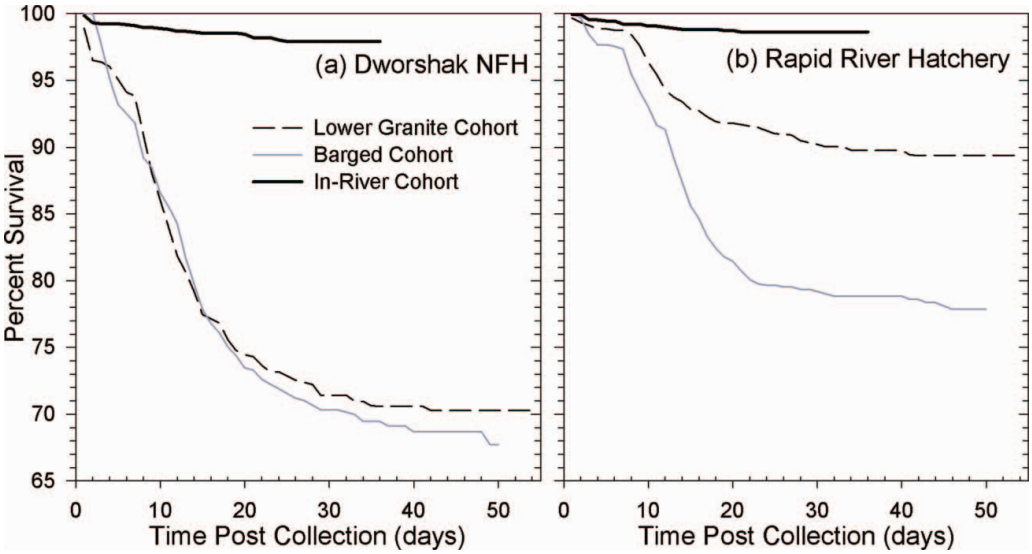

FIGURE 2. Kaplan–Meier survivor comparison of barged, Lower Granite, and in-river cohorts of Chinook salmon originating from **(a)** Dworshak NFH and **(b)** Rapid River Hatchery before challenge with *Listonella anguillarum*.

TABLE 1. Cumulative percent mortality among experimental cohorts of juvenile Chinook salmon and hatcheries before and during disease challenge with *Listonella anguillarum*. The cumulative mortality from before and during challenge is shown in added mortality.

Experimental cohort	Before challenge	During challenge	Added mortality
Lower Granite	18.0 (272/1,507)		
Dworshak NFH	29.2 (184/630)	57.2 (115/201)	86.4
Rapid River Hatchery	10.0 (88/877)	53.5 (161/301)	63.5
Barged	25.0 (380/1,517)		
Dworshak NFH	31.2 (179/573)	58.3 (119/204)	89.5
Rapid River Hatchery	21.3 (201/944)	49.5 (157/317)	70.8
In-River	1.7 (47/2714)		
Dworshak NFH	2.0 (30/1,443)	59.2 (187/316)	61.2
Rapid River Hatchery	1.3 (17/1,271)	58.4 (121/207)	59.7

Pathology screening completed for both hatcheries before release were all negative for IHNV, suggesting that the IHNV infections observed were most probably contracted in the river system during out-migration.

Lethal concentration challenge.—The *L. anguillarum* concentration of 8.0×10^4 CFU/mL resulted in a mean cumulative mortality of 50% in the reference fish 9 d postexposure. This LC50 concentration was considered appropriate for the subsequent exposure concentration during the disease challenge because the cumulative mortalities from the experimental controls and individual hatcheries ranged from 64% to 86%.

Disease challenge.—The survival of Dworshak and Rapid River hatchery fish resulting from exposure to 8.0×10^4 CFU/mL of *L. anguillarum* in the disease challenge is graphically depicted in Figure 3 as a function of time postexposure for barged, Lower Granite, and in-river cohorts. The log-rank chi-square *P*-values associated with different hatchery and cohort Kaplan–Meier survival comparisons are tabulated in Table 2.

TABLE 2. Statistical comparisons (*P*-values of log-rank chi-square tests) of survivorship before and during disease challenge among experimental cohorts based on hatchery of origin and Kaplan–Meier probability estimates.

Comparison	Before challenge	During challenge
Within hatcheries		
Dworshak NFH		
In-river versus barged	<0.001	0.610
In-river versus Lower Granite	<0.001	0.491
Barged versus Lower Granite	0.601	0.868
Rapid River Hatchery		
In-river versus barged	<0.001	0.013
In-river versus Lower Granite	<0.001	0.155
Barged versus Lower Granite	<0.001	0.241
Within cohorts (Dworshak NFH versus Rapid River Hatchery)		
In-River	0.279	0.571
Barged	<0.001	0.010
Lower Granite	<0.001	0.194

There were no significant differences in the survival of fish originating from the Dworshak NFH (Figure 3a; Table 2) during the disease challenge among in-river, barged, and Lower Granite experimental cohorts. For fish originating from Rapid River Hatchery, the survival of the barged cohort was significantly greater than the in-river cohort ($P = 0.013$; Table 2; Figure 3b). The cumulative survival of fish from the barged cohort was also greater than that of the Lower Granite cohort, but the difference was not significant ($P = 0.241$; Table 2). Similarly, the cumulative survival of fish from the Lower Granite cohort was greater than that for fish from the in-river cohort, but the difference was not significant ($P = 0.155$; Table 2).

Comparisons between fish originating from different hatcheries within the same experimental cohort indicated a significant trend of greater disease susceptibility among Dworshak NFH fish than among Rapid River Hatchery fish (Figure 4). Fish within the barged cohort experienced significantly greater survival if they had originated from Rapid River Hatchery compared with those from Dworshak NFH ($P = 0.010$; Table 2). Fish within the Lower Granite cohort also experienced greater survival if they had originated from Rapid River Hatchery compared with those from Dworshak NFH (Figure 4a), but the difference was not significant ($P = 0.194$; Table 2). In contrast, there were no significant differences in survival between hatcheries within the in-river cohort ($P = 0.571$; Table 2).

Physical Status of Out-Migrants

Length and weight description.—Length and weight measurements were obtained for each fish at the time of collection. The mean masses and fork lengths (FLs) of fish after the in-river cohort out-migration at Bonneville Dam were significantly greater than those in the experimental cohorts collected at Lower Granite Dam (barged and Lower Granite; Table 3). Owing to the comparatively short travel time from Lower Granite Dam to Bonneville Dam (36–44 h), no growth was assumed to occur in barged fish. In-river fish from both hatcheries had similar increases in mean FL (5 and 4 mm, respectively) from Lower

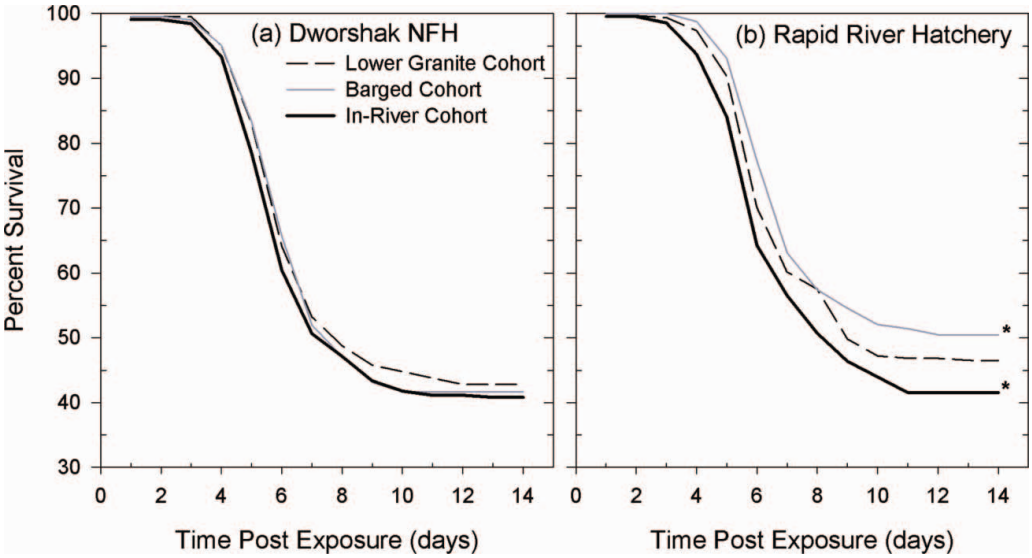

FIGURE 3. Kaplan–Meier survivor comparison of barged, Lower Granite, and in-river cohorts of Chinook salmon originating from **(a)** Dworshak NFH and **(b)** Rapid River Hatchery that were exposed to the LC50 concentration of *Listonella anguillarum*. Asterisks indicate significant differences ($P < 0.05$) between the curves so marked.

Granite Dam to Bonneville Dam, but fish from Dworshak NFH had a three times greater increase in mean weight than fish from Rapid River Hatchery (2.1 and 0.7 g, respectively). However, Rapid River Hatchery fish were significantly larger (mass and length) at Bonneville Dam and Lower Granite Dam than those from the Dworshak NFH population ($P < 0.001$).

Condition factor and lipids.—The mean condition factors of fish were significantly greater for the barged and Lower Granite cohorts collected at Lower Granite Dam than for in-river fish collected at Bonneville Dam (Table 3). Dworshak NFH fish arriving at Lower Granite Dam had significantly lower condition factors than did Rapid River Hatchery fish ($P < 0.001$; Table 3). In contrast, the condition factors for in-river fish at Bonneville Dam were nearly equal for fish originating from both hatcheries ($P > 0.10$). Despite the increase in FL and weight between Lower Granite and Bonneville dams, the mean condition factors decreased for both Dworshak and Rapid River hatchery fish ($P < 0.001$ for both groups). This indicates, in part, a disproportionate increase in length relative to weight.

Mean whole-body total lipids in composite samples of Lower Granite, barged, and in-river fish are summarized in Figure 5. Both Dworshak and Rapid River hatchery fish arriving at Lower Granite Dam had approximately the same mean lipid content (ca. 3.8%) with triglycerides (a major energy store) accounting for 90% of total lipids (data not shown). At Bonneville Dam, in-river fish had a lower total lipid content than experimental cohorts collected at Lower Granite Dam (barged and Lower Granite). There were no significant differences in mean total

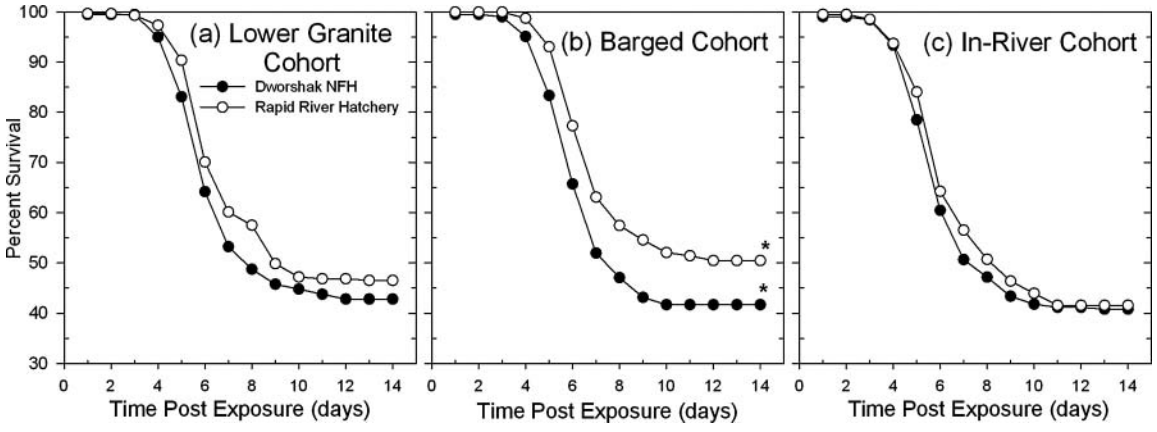

FIGURE 4. Kaplan–Meier survivor comparison of **(a)** barged, **(b)** Lower Granite, and **(c)** in-river cohorts of Chinook salmon originating from Dworshak NFH and Rapid River Hatchery that were exposed to the LC50 concentration of *Listonella anguillarum*. Asterisks indicate significant differences ($P < 0.05$) between the curves so marked.

TABLE 3. Morphological characteristics of Dworshak NFH and Rapid River Hatchery out-migrants based on location of sample collection.

	Fork length (mm)		Weight (g)		Condition factor[a]	
Location and difference	Rapid River Hatchery	Dworshak NFH	Rapid River Hatchery	Dworshak NFH	Rapid River Hatchery	Dworshak NFH
Lower Granite Dam	138 ± 0.5	132 ± 0.5	29.2 ± 0.3	24.4 ± 0.3	1.09	1.06
Bonneville Dam	143 ± 0.4	137 ± 0.4	29.9 ± 0.3	26.5 ± 0.2	1.02	1.03
Difference	5	5	0.7	2.1	0.07	0.03

[a] (Weight × 10^5)/(fork length^3).

lipids for fish originating from the two hatcheries in any of the experimental cohorts. However, the total lipids of Rapid River Hatchery fish had a greater percentage of triglycerides (68%) compared with Dworshak NFH fish (20%) within the in-river cohort.

DISCUSSION

Mortality before and during the disease challenge indicates that yearling Chinook salmon from different hatcheries exist the hydropower system in varying states of health. Fish stocks in varying states of health may influence the occurrence of delayed mortality and the effectiveness of hydropower system management actions to recover listed stocks (e.g., barging versus leaving fish in the river). Differences in health status observed in this study could have originated as a result of different rearing conditions at their respective hatcheries (e.g., feeding regimes, raceway versus pond rearing, and release strategies), as well as out-migration pathways to the first hydropower system dam. However, once the experimental fish entered the hydropower system, fish from Dworshak NFH and Rapid River Hatchery were collected, transported, handled, and held in the laboratory under identical conditions.

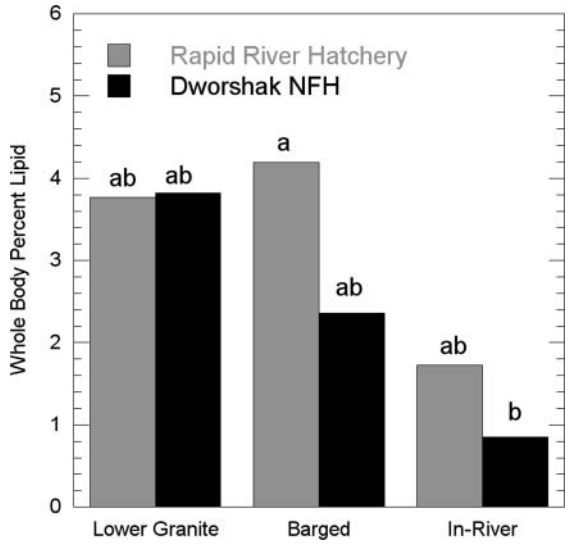

FIGURE 5. Mean percentage of lipids in whole-body composites from Chinook salmon from Dworshak NFH and Rapid River Hatchery at three separate times over their out-migration period. Bars without common letters are significantly different at $P < 0.05$.

Interpretation of Disease Challenge and Prechallenge Mortalities

An interpretation of only the disease challenge results for the 2006 out-migration year is that barging offsets the adverse health effects associated with in-river travel through the hydropower system (and potentially mitigates delayed mortality) only when fish are healthy at the time of barging. For example, if this study had used exclusively fish from Rapid River Hatchery, we would conclude that the hydropower system adversely affects the health of out-migrants entering the estuary, owing to greater disease challenge mortality within the in-river cohort than the barged cohort. We would also conclude that barging maintains the health of out-migrants entering the estuary in a state comparable with fish passing Lower Granite Dam. This outcome is identical to the study conducted during the 2002 out-migration year with Rapid River Hatchery fish (Arkoosh et al. 2006); hence, the finding was reproducible across different brood and out-migration years. In contrast to the findings of Arkoosh et al. (2006) and the present results with Rapid River Hatchery fish, fish originating from the Dworshak NFH had no differences in disease challenge mortality between the in-river and barged cohorts. If this study had used exclusively fish from Dworshak NFH, we would conclude that the hydropower system and barging have either no effect or equivalent effects on the health of out-migrants entering the estuary. Consequently with Dworshak NFH fish, we would conclude that there is no benefit to barging out-migrant Snake River spring Chinook salmon other than preventing in-river direct mortality. Therefore, the hatchery of origin is a critical variable affecting the conclusions drawn from studies designed to understand the significance of various mitigation strategies.

Owing to disproportionately greater mortality in the barged and Lower Granite cohorts than the in-river cohort in the laboratory before the disease challenge, the disease challenge results alone must be interpreted with caution when characterizing the effect of barging versus in-river out-migration. The barged and Lower Granite cohort populations in the disease challenge may have been biased as a result of the greater prechallenge mortality, putatively associated with disease. Similarly, there were greater prechallenge mortalities among Dworshak NFH fish within the

barged and Lower Granite cohorts than Rapid River Hatchery fish from the same cohorts. However, within the in-river cohort, there were no differences in prechallenge mortalities between hatcheries.

Although there is no method to explicitly quantify the bias that may have occurred between cohorts and hatcheries, one approach would be to add the percent mortality that occurred before the challenge to the percent mortality that occurred during the disease challenge. This addition is presented in Table 1 alongside the observations of cumulative mortality before and after the disease challenge. If the disease challenge survival data are compensated for biased populations in this manner, we find that the differences between hatcheries remain for a given cohort, but the interpretation of the effect of barging based on the disease challenge results alone has changed. Specifically, fish originating from Dworshak NFH had greater mortality than fish originating from Rapid River Hatchery in both barged and Lower Granite cohorts, but there was no difference in in-river cohorts. The differences in mortality suggest that the Dworshak NFH fish were actually less healthy than the Rapid River Hatchery fish at the time of barging (barged and Lower Granite cohorts), but those differences were eliminated during hydropower system in-river out-migration (in-river cohort).

In contrast, an interpretation of the effect of barging for fish with different out-migration histories based on the added mortality presented in Table 2 is different from the interpretation based solely on the disease challenge outcome. For example, the added prechallenge and disease challenge mortality among the barged cohorts was greater than the added mortality among the in-river cohorts for fish originating from both hatcheries. Consequently, the differences in mortality suggest that fish from both hatcheries that were barged were actually less healthy than the in-river fish and that barging did not provide a benefit. This outcome was due to significantly greater prechallenge mortalities in the barged cohort than in the in-river cohort, again suggesting that barging will only offset the adverse health effects associated with in-river travel through the hydropower system (and potentially mitigating delayed mortality) when fish are healthy at the time of barging.

Trends of Fish Characteristics during Out-Migration and Subsequent Mortalities

Trends were observed between fish FL and weight measured during out-migration and differences in mortality before and during the disease challenge. Fish from Rapid River Hatchery were significantly larger than fish from Dworshak NFH at Lower Granite Dam and had significantly less prechallenge mortality among Lower Granite and barged cohorts and significantly less disease challenge mortality among barged cohorts. Also, in-river fish from Dworshak NFH and Rapid River Hatchery were significantly larger when collected at Bonneville Dam than were fish in barged and Lower Granite cohorts and experienced significantly less prechallenge mortality. However, there were no significant differences in prechallenge or disease challenge mortalities between fish originating from the two hatcheries within the in-river cohort, despite significant differences in size at collection. There were also no differences in condition factors for in-river fish from Dworshak NFH and Rapid River Hatchery. The decrease in condition factor during in-river out-migration indicates a greater increase in length and a uniformity of mass-to-length proportion among fish from both hatcheries that was not present at Lower Granite Dam.

A general trend was observed between lower lipid levels in fish during out-migration and increased disease susceptibility during the disease challenge, but not in prechallenge mortalities. Once held in the laboratory, fish from all cohorts were fed a daily ration, resulting in fish growth (data not shown) and presumably an increase in total lipids, which potentially confounds relationships with mortality. Previous studies suggest that energy and energy stored as lipids (e.g., triglycerides) are important factors to consider when examining the survival of juvenile salmonids (Biro et al. 2004; Finstad et al. 2004). Although differences in diet and feeding regimes may have existed at Dworshak NFH and Rapid River Hatchery, the lipid levels of fish sampled at Lower Granite Dam were equivalent. After Lower Granite Dam, the total lipids and triglyceride levels in fish from both hatcheries decreased among fish within the in-river cohort with greater losses observed among fish originating from Dworshak NFH. Lipid levels decrease, in part, owing to the metabolic demands associated with smoltification (Beckman et al. 2000; Meador et al. 2006). Juvenile salmon are known to have lipid levels decrease to 1–3% during smoltification (Meador et al. 2006), suggesting that the mean levels found in the in-river fish originating from Rapid River Hatchery would be normal (1.72%), but that the mean levels found in the in-river fish originating from Dworshak NFH were below normal (0.85%). Although no similar study has been completed with juvenile Chinook salmon, a critical lipid threshold of 1% has been associated with increased mortality in juvenile rainbow trout (Biro et al. 2004).

We have identified a trend of better health among Rapid River Hatchery fish than among Dworshak NFH fish within the barged and Lower Granite cohorts. Although the mortalities before the disease challenge were putatively associated with disease and the mortalities within the disease challenge were due to controlled exposure to a virulent salmonid pathogen, we have not isolated the specific cause or difference in health between the two hatcheries. Based on the timing of the highest laboratory mortalities, out-migration timing may be related to health of the fish populations in the hydropower system, which could be related to high loading densities in barges at the peak of out-migration and disease transmission. Although hatcheries perform pathogen screens before fish are released and other studies have investigated the prevalence of *Renibacterium salmoninarum* at different locations in the out-migration corridor (Sanders et al. 1992; Maule et al. 1996; Elliott et al. 1997;

Arkoosh et al. 2004), only one study has compared the presence of pathogens in fish with different out-migration histories (Van Gaest et al. 2011). Van Gaest et al. (2011) did find greater prevalence of pathogens in fish with barging out-migration histories than in-river out-migration histories. The effect of individual length, weight, and lipid differences on disease susceptibility during the disease challenge were possibly diminished owing to the laboratory holding periods before the disease challenge. However, the differences in biological characteristics between Dworshak NFH and Rapid River Hatchery fish that were measured during out-migration were only intended to provide additional metrics related to health of the stocks.

2006 Out-Migrant Adult Returns and Delayed Mortality

For the 2006 out-migration year, we found that there were differences in hatchery stocks at the time of barging that could affect an assessment of hydropower system mitigation efforts. Condensing the observations collected during out-migration and the mortalities observed before and during the disease challenge, the outcomes from this study are in agreement with estimates of delayed mortality based on returning adults from the 2006 out-migration year. In this study, Rapid River Hatchery fish were found to be healthier than Dworshak NFH fish in barged and Lower Granite cohorts, Likewise, adult returns revealed significantly greater SAR rates among Rapid River Hatchery fish (0.58%) that were barged through the hydropower system compared with Dworshak NFH fish (0.35%) during the 2006 out-migration (DeHart et al. 2009). In addition, the posthydropower system differential mortality (D) for Rapid River Hatchery fish (0.85) was also significantly greater than the D-value for Dworshak NFH fish (0.57) that out-migrated in 2006 (DeHart et al. 2009). In this study no differences in prechallenge or disease challenge mortalities were found between in-river fish originating from these hatcheries. Similarly, adult returns revealed that the two hatcheries had nearly equivalent in-river SARs for fish that out-migrated from Rapid River Hatchery (0.42%) and Dworshak NFH (0.39%) during 2006 (DeHart et al. 2009). In addition, reach survival estimates (V_{ir}) from Lower Granite Dam to Bonneville Dam were nearly equivalent for fish with in-river out-migration histories originating from Rapid River Hatchery (0.55) and Dworshak NFH (0.54) during 2006 (DeHart et al. 2009). Consequently, the hydropower system appears to have a normalizing effect on the differences between these stocks. Given that barge survival (V_{brg}) is also assumed to be equal (0.98) for all fish transported, any difference in D of barged and in-river fish from Dworshak NFH and Rapid River Hatchery fish was probably due to a difference in the adult survival of fish that were barged. Although both hatcheries have D-values less than 1, only the value for Dworshak NFH is significantly less than 1 (90% confidence interval, 0.41–0.81; DeHart et al. 2009). Consequently, delayed mortality is greater among barged fish than in-river fish originating from Dworshak NFH, but there was no difference in the delayed mortality of barged and in-river fish originating from Rapid River Hatchery. This outcome is identical to our conclusions based on the additive mortalities before and during the disease challenge.

We recognize that there are a number of factors that may be contributing to differential delayed mortality. Our observations highlight the importance of considering out-migrant health, stock origin, and out-migration pathways to the first dam in management decisions within the hydropower system. Additional factors, such as the timing of estuary and ocean entry and size-selective predation (Williams et al. 2005; Muir et al. 2006), may also be selectively affecting barged fish relative to in-river fish or one fish stock relative to another, which would be exacerbated for fish in poor health. If differences in D and SARs are affected by health differences between hatcheries at the time of barging, the evaluation of the mitigative benefit of barging would also be affected. In this case, an evaluation of barging that considered only Rapid River Hatchery fish would conclude that barging did not affect delayed mortality. Whereas, an evaluation of barging that considered only Dworshak NFH fish would conclude that barging adversely affected delayed mortality. Incorporating stock origin as a factor that may affect the assessment of mitigation efforts is divergent to management strategies that currently pool run-of-river stocks. Future studies are needed to refine and quantify the importance of fish health and infectious diseases as an indicator of health in out-migrant Snake River spring Chinook salmon, as well as the effect of selected mitigation strategies on fish health and the introduction and transmission of infectious diseases.

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REFERENCES

Arkoosh, M. R., D. Boylen, C. L. Stafford, L. L. Johnson, and T. K. Collier. 2005. Use of disease challenge assay to assess immunotoxicity of xenobiotics. Pages 19–38 *in* G. K. Ostrander, editor. Techniques in aquatic toxicology. Taylor and Francis, New York.

Arkoosh, M. R., E. Clemons, A. N. Kagley, C. Stafford, A. C. Glass, K. Jacobson, P. Reno, M. S. Myers, E. Casillas, F. J. Loge, L. L. Johnson, and T. K. Collier. 2004. Survey of pathogens in juvenile salmon *Oncorhynchus* spp. migrating through Pacific Northwest estuaries. Journal of Aquatic Animal Health 16:186–196.

Arkoosh, M. R., A. N. Kagley, B. F. Anulacion, D. Boylen, B. P. Sandford, F. J. Loge, L. L. Johnson, and T. K. Collier. 2006. Disease susceptibility of hatchery Snake River spring Chinook salmon (*Oncorhynchus tshawytscha*) with different juvenile migration histories in the Columbia River. Journal of Aquatic Animal Health 18:223–231.

Beckman, B. R., D. A. Larsen, C. Sharpe, B. Lee-Pawlak, C. B. Schreck, and W. W. Dickhoff. 2000. Physiological status of naturally reared juvenile spring Chinook salmon in the Yakima River: seasonal dynamics and changes associated with smolting. Transactions of the American Fisheries Society 129:727–753.

Berggren, T., H. Franzoni, L. Basham, P. Wilson, H. Schaller, C. E. Petrosky, E. Weber, R. Boyce, and N. H. Bouwes. 2003. Comparative survival study (CSS) of PIT-tagged spring Chinook. 2002 Annual Report to the Bonneville Power Administration, contract 8712702, Portland, Oregon. Available: www.fpc.org. (November 2009).

Berggren, T., P. McHugh, P. Wilson, H. Schaller, C. Petrosky, E. Weber, and R. Boyce R. 2006. Comparative survival study (CSS) of PIT-tagged spring–summer Chinook and summer steelhead. 2006 Annual Report to the Bonneville Power Administration, contract 199602000, Portland, Oregon. Available: www.fpc.org. (November 2009).

Biro, P. A., A. E. Morton, J. R. Post, and E. A. Parkinson. 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 61:1513–1519.

Bouwes N. H., H. Schaller, P. Budy, C. Petrosky, R. Kiefer, P.Wilson, O. Langness, E. Weber, and E. Tinus. 1999. An analysis of differential delayed mortality experienced by stream-type Chinook salmon of the Snake River. Oregon Department of Fish and Wildlife, Technical Report, Portland.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35–51.

Congleton, J. L., W. J. LaVoie, C. B. Schreck, and L. E. Davis. 2000. Stress indices in migrating juvenile Chinook salmon and steelhead of wild and hatchery origin before and after barge transportation. Transactions of the American Fisheries Society 129:946–961.

DeHart, M., J. Tuomikoski, J. McCann, T. Berggren, H. Schaller, P. Wilson, S. Haeseker, C. Petrosky, E. Tinus, T. Dalton, and R. Ehlke. 2009. Comparitive survival study (CSS) of PIT-tagged spring/summer Chinook and summer steelhead. Annual Report to the Bonneville Power Administration, Contract 19960-200, Portland, Oregon.

Elliott, D. G., R. J. Pascho, L. M. Jackson, G. M. Matthews, and J. R. Harmon. 1997. *Renibacterium salmoninarum* in spring-summer Chinook salmon smelts at dams on the Columbia and Snake rivers. Journal of Aquatic Animal Health 9:114–126.

Finstad, A. G., O. Ugedal, T. Forseth, and T. F. Naesje. 2004. Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 61:2358–2368.

Maule, A. G., D. W. Rondorf, J. Beeman, and P. Haner. 1996. Incidence of *Renibacterium salmoninarum* infections in juvenile hatchery spring Chinook salmon in the Columbia and Snake rivers. Journal of Aquatic Animal Health 8:37–46.

Meador, J. P., F. C. Sommers, G. M. Ylitalo, and C. A. Sloan. 2006. Altered growth and related physiological responses in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from dietary exposure to polycyclic aromatic hydrocarbons (PAHs). Canadian Journal of Fisheries and Aquatic Sciences 63:2364–2376.

Muir, W. D., D. M. Marsh, B. P. Sandford, S. G. Smith, and J. G. Williams. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook: unraveling the mystery. Transactions of the American Fisheries Society 135:1523–1534.

Muir, W. D., S. G. Smith, J. G. Williams, and E. E. Hockersmith. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers. North American Journal of Fisheries Management 21:269–282.

Nash, R. D. M., A. H. Valencia, and A. J. Geffen. 2006. The origin of Fulton's condition factor: setting the record straight. Fisheries 31:236–238.

Noga, E. J. 1996. Fish disease: diagnosis and treatment. C. V. Mosby, St. Louis, Missouri.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academic Press, Washington, D.C.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1–24.

Ruckelshaus, M., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33:665–706.

Sanders, J. E., J. J. Long, C. K. Arakawa, J. L. Bartholomew, and J. S. Rohovec. 1992. Prevalence of *Renibacterium salmoninarum* among downstream-migrating salmonids in the Columbia River. Journal of Aquatic Animal Health 4:72–75.

Sandford, B. P., and S. G. Smith. 2002. Estimation of smolt-to-adult return percentages for Snake River salmonids, 1990–1997. Journal of Agricultural, Biological, and Environmental Statistics 7:243–263.

Schreck, C. B., T. P. Stahl, L. E. Davis, D. D. Roby, and B. J. Clemens.2006. Mortality estimates of juvenile spring-summer Chinook salmon in the lower Columbia River and estuary, 1992–1998: evidence for delayed mortality? Transactions of the American Fisheries Society 135:457–475.

Sindermann C. J. 1990. Principal diseases of marine fish and shellfish. Academic Press, New York.

USFWS and AFS–FHS (U.S. Fish and Wildlife Service and American Fisheries Society–Fish Health Section). 2005. Standard procedures for aquatic animal health inspections. *In* AFS–FHS. FHS blue book: suggested procedures for the detection and identification of certain finfish and shellfish pathogens, 2005 edition. AFS–FHS, Bethesda, Maryland.

Van Gaest, A. L., J. P. Dietrich, D. E. Thompson, D. A. Boylen, S. A. Strickland, T. K. Collier, F. J. Loge, and M. R. Arkoosh 2011. Survey of pathogens in hatchery Chinook salmon with different outmigration histories through the Snake and Columbia rivers. Journal of Aquatic Animal Health 23.

Waples, R. S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 48:124–133.

Wedemeyer, G. A. 1996. Physiology of fish in intensive culture. Chapman and Hall, New York.

Williams, J. G., S. G. Smith, and W. D. Muir. 2001. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower systems, 1996–1980 and 1993–1999. North American Journal of Fisheries Management 21:310–317.

Williams, J. G., S. G. Smith, R. W. Zabel, W. D. Muir, M. D. Scheuerell, B. P. Sandford, D. M. Marsh, R. A. McNatt, and S. Achord. 2005. Effects of Federal Columbia River Power System on salmonid populations. NOAA Technical Memorandum NMFS-NWFSC-63.

Ylitalo, G. M., G. K. Yanagida, L. C. Hufnagle, and M. M. Krahn. 2005. Determination of lipid classes and lipid content in tissues of aquatic organisms using thin layer chromatography/flame ionization detection (TLC/FID) microlipid method. Pages 449–464 *in* G. K. Ostrander, editor. Techniques in aquatic toxicology, volume 2. CRC Press, Boca Raton, Florida.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice-Hall, Englewoods Cliffs, New Jersey.